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RICE GENE SYMBOLIZATION AND LINKAGE GROUPS

Agricultural Research Service
U. S. DEPARTMENT OF AGRICULTURE

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RICE GENE SYMBOLIZATION AND LINKAGE GROUPS[1]

I. STANDARDIZATION OF GENE SYMBOLS IN RICE[2]

Introduction

Intensified research programs in rice genetics are fully justified by the importance of the crop. Generally, rice geneticists are immersed in breeding urgently needed improved rice varieties with scant time for the basic genetic studies needed for the fullest appreciation of the species and ultimately for continued progress in the development of new varieties.

Rice genetics, however, is retarded also by language barriers and isolation of the workers. One unfortunate result is a confusing lack of uniformity in symbols used to designate genes. Agreement is needed on standardized symbols for known genes and on general rules for assigning symbols to additional genes as they are found.

The first worker to propose standard symbols for rice genes probably was Yamaguchi (8)[3] in 1927, but he did not suggest a guide for devising additional symbols. Kadam and Ramiah (6) in 1943 proposed certain rules for the symbolization of genes in rice and listed recommended symbols as far as possible. Their system was followed in the United States, but in Japan a quite different set of symbols for the same or similar genes came into use. The resulting impasse is not easily compromised; realizing this, the Sixth (1955) Meeting of the FAO International Rice Commission Working Party on Rice Breeding (1, pp. 19-20) appointed a committee to report on standardization of gene symbolization and, also, to report on linkage groups.[1]

International Rules for Standardization of Gene Symbols

Fortunately, a guide to eventual uniformity of usage by rice geneticists is found in a set of rules for developing standardization in genetic symbols. These rules for work with all crops were adopted by the Tenth (1958) International Congress of Genetics (5). The investigating committee, headed by Y. Tanaka, had reported its recommended rules in

[1] This publication constitutes the complete report of the Committee on Nomenclature and Linkage Groups appointed by the Sixth (1955) Meeting of the FAO International Rice Commission Working Party on Rice Breeding to report on linkage groups and the standardization of gene symbols. In 1959 an initial list of recommended symbols was submitted to and approved by the continuing working party then under the new name of Working Party on Rice Production and Protection. The members of the committee were Nelson E. Jodon, Chairman, with the U. S. Department of Agriculture, Agricultural Research Service, Rice Experiment Station, Crowley, La.; Dr. Seijin Nagao, with Hokkaido University (Japan), Plant Breeding Institute, Sapporo; and Dr. N. Parthsarathy, formerly with the Department of Agriculture in India, as Director of Central Rice Research Institute, Cuttack. Circumstances caused the task of preparing the tabulations for Japan and India to devolve, respectively, on Dr. Man-emon Takahashi, an associate of Dr. Nagao, and on Dr. R. Seetharaman, Central Rice Research Institute, who had the advice of Dr. K. Ramiah. Mr. Jodon made the tabulations for the United States and assembled the report. The Committee is indebted to Drs. D. W. Robertson and Warren H. Leonard of Colorado State University for reviewing the manuscript.

[2] The list of recommended gene symbols for rice was agreed upon after an extensive exchange of correspondence by members of the Committee.

[3] Numbers in parentheses (or brackets) refer to Literature Cited, p. 4.

1957 (4). Two pertinent paragraphs from the introductory part of the report may be quoted:

> It is the opinion of the committee that standardization of symbols and adoption of common rules, although they cannot and should not be made compulsory, are highly desirable whenever possible. Adherence to some standard system would lessen confusion and greatly facilitate communication between specialists in different areas of genetics. In general, the recommendations listed below are based on established practices and are broad enough to be used for diverse situations.
>
> * * * * * * *
>
> It is clear that periodic revisions of nomenclatorial conventions will be called for by the progress of genetics. It is suggested, therefore, that this task be assigned by each Genetic Congress to a committee representing microbial, plant, animal and human genetics. This committee should also encourage the preparation of lists of currently used symbols for genetically important forms by the investigators working with these organisms.

The rules adopted by the International Congress of Genetics (3,4) are given below, along with the comments on the application to rice genetics which were added to follow some of the rules (3).

1. In naming hereditary factors, the use of languages of higher internationality should be given preference. (English is and probably will continue to be the language most commonly used by rice geneticists.)

2. Symbols of hereditary factors, derived from their original names, should be written in Roman letters of distinctive type, preferably in italics, and be as short as possible. (Symbols may be based on a key word or on an adjective-noun combination.)

3. Whenever unambiguous, the name and symbol of a dominant begin with a capital letter and those of a recessive with a small letter. (Non-controversial.)

4. Literal or numeral superscripts are used to represent the different members of an allelic series. (Same as 'convention' number 1 of Kadam and Ramiah [6].)

5. Standard or wild type alleles are designated by the gene symbols with + as a superscript or by + with the gene symbol as a superscript. In formulae the + alone may be used. (It hardly could be said that there is either a standard or a wild type in rice, and therefore the first part of this rule does not seem to apply. The + sign could be used in formulae if desired.)

6. Two or more genes having phenotypically similar effects are designated by a common basic symbol. Non-allelic loci (mimics, polymeric genes, etc.) are distinguished by an additional letter or Arabic numeral either on the same line after a hyphen or as a subscript. Alleles of independent mutational origin may be indicated by a superscript. (Here rice geneticists might follow 'convention' numbers 2 and 3 of Kadam and Ramiah [6] in using literal subscripts for complementary genes and numeral subscripts for duplicate genes.)

7. Inhibitors, suppressors and enhancers are designated by the symbols I, Su, and En, or by i, su, and en if they are recessive, followed by a hyphen and the symbol of the allele affected. (This appears non-controversial.)

8. Whenever convenient, lethals should be designated by the letter l or L, and sterility and incompatability genes by s or S. (Would not be needed for albinos, which are always lethal.)

9. Linkage groups and corresponding chromosomes are preferably designated by Arabic numerals. ([In the past] Roman numerals have been used, but in the future this rule should be complied with.)

10. The letters X and Y are recommended to designate the sex chromosomes. (Does not apply.)

11. Genic formulae are written as fractions with the maternal alleles given first or above. Each fraction corresponds to a single linkage group. Different linkage groups written in numerical sequence are separated by semicolons. Symbols of unlocated genes are placed within parentheses at the end of the formula. In euploids and aneuploids the gene symbols are repeated as many times as there are homologous loci. (Non-controversial.)

12. Chromosomal aberrations should be indicated by the abbreviations: Df for deficiency, Dp for duplication, In for inversion, T for translocation, Tp for transposition. (Cytologists and cytogeneticists will have use for these symbols in future work with rice.)

13. The zygotic number of chromosomes is indicated by 2n, the gametic number by n and the basic number by x. (Non-controversial usage.)

14. Symbols of extra-chromosomal factors should be enclosed within brackets and precede the genic formulae. (Non-controversial usage.)

Work Relating to the Recommendation of Gene Symbols for Rice

A survey of inheritance studies in rice was made by the International Rice Commission Committee, preparatory to the selection of gene symbols conforming to the rules of the International Congress of Genetics. Data published before 1943 had been summarized in brief tabular form by Kadam and Ramiah (6) in their "Symbolization of Genes in Rice" (1943); over the past 20 years their Appendix III has served as a model for the summarization of new findings.

Included in this report as Table 1 is an abridgement of the tabulation by Kadam and Ramiah (6) in their Appendix III, anthocyanin plant colors here being omitted. Table 2 is a tabulation of Indian data before 1943 as discussed by Ramiah and Rao (7) in "Rice Breeding and Genetics" (1953), including the very extensive work on inheritance of plant colors. The more recent data from India are collected in Table 3.

Genetic studies in Japan since about 1940 are collected in Table 4; those in the United States during the same period are collected in Table 5.

Each table shows the characters segregating, the gene symbols recommended for future use, the original symbols, and the segregation ratios, and refers to the original publications. Following each table is a list of references. The tabulations and reference lists, together with the linkage information in the second part of this report, make up a concise, though not complete, survey of rice genetic data to date.

The alphabetical list of recommended symbols is included following this section and preceding the summary tables. Symbols were not selected entirely for qualitative characters, nor for cytoplasmic (maternal) inheritance. They were assigned in accordance with the rules of the International Congress of Genetics for numerous Mendelian (quantitative) characters, especially those which may be useful as marker genes.

The objective of this Committee was to set a pattern for future use rather than to set up a complete list of symbols. The recommended symbols are not necessarily complete genic formulae for complex characters, but are intended as a basis for symbolization as

the need arises. Symbols used by the original authors reviewed were revised when necessary to bring about uniformity under the above rules of the International Congress of Genetics. If the original author did not use symbols or the members of the Committee were not familiar with a character, no recommended symbols were proposed. The proposal of symbols for characters not so identified is left to the workers who will use the characters in future studies.

The list of symbols as revised was submitted in a report to the Eighth (1959) Meeting of the FAO International Rice Commission Working Party on Rice Production and Protection (2, pp. 10-11). The report was adopted with the recommendation that the revised symbols be accepted as standard usage by rice geneticists and that additional gene symbols be assigned by workers, as needed, in conformity with rules of the International Congress of Genetics. The list of the symbols, published in the News Letter of the International Rice Commission in December 1959 (3), has been further revised by the Committee in preparing this report. During the period of transition to the use of the recommended symbols, rice geneticists should indicate in their publications the important previously employed symbols.

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2. FAO International Rice Commission Working Party on Rice Production and Protection (1960). Report of Eighth Meeting, Peradeniya, Ceylon, Dec. 1959, 50 pp. (Same Committee as above.)

3. FAO International Rice Commission Committee on Nomenclature and Linkage Groups (1959). Genetic symbols for rice recommended by the International Rice Commission. News Letter Internatl. Rice Comm. 8 (4): 1-7.

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Gene Symbols Recommended For Rice[4]

A

A, A^d, a	= allelic anthocyanin activator genes (complementary action with C genes produces red or purple in apiculus)
al	= albino*
An	= Awned*
au	= rudimentary auricle

B

bc	= brittle culm
Bd	= Beaked hull (tip of lemma recurved over palea)
Bf	= Brown furrow (dark brown color in furrows of lemma and palea). See H^f
I-Bf	= Inhibitor of dark brown furrow
bg	= coarse (big) culms
Bh	= Blackhull (complementary genes)*
bl	= physiologic diseases showing dark brown or blackish mottled discoloration of leaf
bn	= bent node - culm forms angle at node

C

C, C^B, C^{Bp}, C^{Bt}, C^{Br}, c	= allelic basic genes for anthocyanin color; higher alleles have pleiotropic expression in internode
C alone	= tawny colored apiculus
CA	= red or purple colored apiculus
CAP	= completely and fully purple colored apiculus
En-C	= Enhancer of C
Ce	= Cercospora resistance
chl	= chlorina (chlorophyll deficiency)
Cl	= Clustered spikelets, also super cluster
cls	= cleistogamous spikelets
clw	= claw shaped spikelets. See tri and Bd

D

d	= dwarfs,* about 1/3 to 1/2 height or normal; discrete classes in segregating populations
da	= double awn
Dn	= Dense or "compact"; very close arrangement of spikelets (vs. normal panicle); epistatic to Ur. See Lx, also Cl
Dn_2	= Dense vs. lax
Dn_3	= Normal vs. lax
Dp	= Depressed palea and underdeveloped palea
dw	= deep water paddy, so-called floating rice

E

Ef	= Early flowering (low photosensitivity).* See Lf
En-	= Enhancer (intensifier). Precedes symbol of character affected
er	= erect growth habit, recessive to spreading or procumbent. See dw, la
Ex	= Exerted vs. enclosed panicle

F

Fgr	= Fragant flower
fs	= fine stripe

[4] Recommended by the Eighth (1959) FAO International Rice Commission Working Party on Rice Production and Protection (2); the list includes present revisions.

*More than one gene involved; subscripts to be supplied by workers as needed. Letter subscripts are suggested for complementary genes, numeral subscripts for genes having phenotypically similar effects and also for polymeric genes. See rule 6.

G

g	= long glume* exceeding 1/3 length of the spikelet
gh	= goldhull (golden yellowhull, recessive to straw color). See Wh
gl	= glabrous (non-hairy) leaf. See Lh
Gm	= semi-dominant long glume. More extreme and less regular in expression than g. Epistatic to g

green and white stripe; see fs, v.

H

(H or h is suggested to denote hull, i.e. lemma and palea.)

H^m, H^i, Hg, H^f	= allelic genes for non-anthocyanin colors of lemma and palea appearing only in the presence of Gh; goldhull colors appear with gh
He	= Helminthosporium resistance
hsp	= hullspot

I

I	= positive vs. negative staining with iodine-potassium iodide solution
I-	= inhibitor (precedes symbol of character inhibited)

K

(K or k is suggested to denote kernel, i.e. caryopsis.)

L

(l (as second letter of a symbol) is suggested to denote leaf.)

l-	= lethal (precedes symbol of character having lethal effect)
la	= lazy. See er
Ld	= Lodging
Lf	= Late flowering (highly photosensitive).* See Ef
lg	= liguleless (auricle and collar also absent)*
Lh	= very hairy (long hair) dominant to ordinary pubescence. See gl
lk	= grain length (long grain)*
lmx	= extra lemma
lu	= lutescent
Lx	= Lax vs. normal panicle. See Dn
Lx_2	= Lax vs. compact

M

me	= multiple embryos (poly-embryonic)
mp	= multiple pistils (poly-caryoptic)

mottled leaf; see bl

N

nal	= narrow leaf
nl	= neckleaf
nk or I-Nk	= notched kernel

O

o	= open hull (parted lemma and palea)

P

(P (as first letter of a symbol) is suggested to denote anthocyanin color.) Exceptions: Ph, Pi

P	= Completely purple apiculus (complementary action with C and A)
Pau	= Purple auricle, basic to Plg
Pg	= Purple outerglumes
Ph	= Phenol staining of hull and bran
Pi	= Piricularia resistance
Pin	= Purple internode. See C
Pl	= Purple leaf. See Pw
Pla	= Purpleleaf apex (complementary action with C and A)

Plg = Purple ligule. See Pau
I-Pl = colorless leaf except margin
Pn = Purplenode
Pr = Purplehull (lemma and palea)(complementary action with CAP)
Prp = Purple pericarp
Ps = Purple stigma (complementary action with CAP)
Psh = Purple sheath
Pu = Purple pulvinus
Pw = Purplewash. See Pl
Px = Purple axil

R

Rc = Brown pericarp (basic to Rd)
Rd = Red pericarp (complementary action with Rc)
ri = verticillate (whorled) arrangement of rachis ("rinshi" character)
Rk = Round spikelet (kernel)
rl = rolled leaf

S

s = sterility*
Sc = Sclerotium oryzae resistance
Se = Photosensitivity. See Ef, also Lf
Sh = Dominant shattering as in drop-seed or wild types vs. difficult or intermediate threshing. See th
Sk = Scented kernel
sn = sinuous neck. See Ur
spr = spreading panicle branches

spreading growth habit; see er, also la
superclustered spikelets; see Cl

T (T is suggested to denote plant height ("Tallness") except where controlled by dwarfing genes.) See d

I-T = short non-dwarf plant vs. tall
tb = tipburn yellow
Tf = Tough dehulling
th = shattering or easy threshing recessive to difficult separation. See Sh
tl = twisted leaves
tri = triangular hull (spikelet). See clw

U

Ur = Undulate rachis vs. normal. See sn

V

v = virescent, also green and white stripe. See fs

W

wb = white belly (endosperm)
wb_2 = white core (endosperm)
Wh^2 = Whitehull, epistatic to gh
wx = waxy (glutinous) endosperm

Y

y = yellow leaf
l-y = lethal yellow, also xantha*

Z

z = zebra stripe

Recommendations Concerning Specific Reported Symbolization From Various Countries

Table 1. Inheritance of genetic characters in rice other than anthocyanin colors, reported prior to 1943, relating to the symbolization proposed by Kadam and Ramiah in their 1943 study, Symbolization of Genes in Rice,[1] and to a recommended symbolization

Characters	Symbols		Segregation ratios	Author reporting segregation[2]
	Recommended	Kadam & Ramiah proposal		
A. Presence or absence of structures				
Awned	An	An	3:1, 15:1, 9:7?, 9:6:1, 12:3:1, 12:1:2:1	5, 6, 8, 12, 18, 20, 36, 47, 53, Kato 1916[3]
Awn Inhibitor	I-An	Ian	13:3	8
Auricle present or absent (see ligule).				
Collar or junctura present or absent (see ligule).				
Liguleless	lg	lg	3:1	20, 42, 60, 84
Multiple pistils	mp	mp	3:1	59
B. Size				
Long outer glumes	g	g_1, g_2	3:1, 1:2:1, 15:1	5, 6, 53, 57, 59, 63
Short vs. long spikelet (kernel length).	lk	kl	1:2:1, 3:1, 9:7	6, 9, 57, 69, 78
Dwarf	d	d, d_1-d_5	3:1	2, 20, 26, 50, 58, 65, 79
Tall (i.e. long vs. short culms)	T	t	3:1	2, 65, 66, 67
Short (i.e. short vs. long culms)	T, I-T?	It	3:1, 13:3(?)	65, 66, 67
Normal vs. large spikelets			3:1	81

[1] Table is an adaptation from: Kadam, B. S., and Ramiah, K. (1943). Symbolization of genes in rice. Indian J. Genet. & Plant Breed. 3: 7-27, 125-132.

[2] Numbers refer to a list of references following this table. The references in the main are part of the bibliography of the above article.

[3] Reported in an address by Dr. H. Ando. This was published in Bul. Dept. Agr. Japan. 2: 1-102. 1916.

[4] See table footnote 3, p. no. 8

Table 1. Continued

Characters	Symbols		Segregation ratios	Author reporting segregation[2]
	Recommended	Kadam & Ramiah proposal		
C. Modification of structures, composition, and growth habit				
Round or oval spikelet vs. normal.	Rk	kr_{al}, kr_b	3:1, 9:7	6, 63
Easy vs. tough dehulling	Tf, I-Tf?	Itf	3:1	54
Tough vs. easy dehulling	Tf	Tf	3:1	54
Normal vs. parted lemma & palea (open hull).	o	hpt	3:1	35
Lax vs. compact panicle	Lx	Lx	3:1	4, 47, 63
Lax vs. normal panicle	Lx		3:1	80
Non-spreading vs. spreading panicle.	spr	spra, sprb	9:7	36
Partly emerged vs. tip emerged vs. enclosed panicle.	Ex	ex_1-ex_3	49:3:12	76
Normal vs. sinuous neck	sn	ne_1, ne_2	15:1	19
Non-clustered vs. clustered spikelets.	?	cl	3:1	59, 63
Clustered vs. non-clustered	Cl		1:2:1	63
Shattering vs. non-shattering	Sh	sh_1, sh_2	15:1	25
Difficult vs. easy threshing	th	Ish	3:1	20
Vitreous (or starchy) vs. waxy (glutinous) endosperm.	wx	wx	3:1	17, 56, 63, 83
Vitreous vs. opaque soft starch (white core).	wb_2	Op	3:1	10
Vitreous vs. "white belly"	wb	Wb	3:1	11
Normal vs. rolled leaf	rl	Lro	3:1	44
Normal vs. twisted leaf	tl	Ltw	3:1	27
Normal vs. brittle culm	bc	bc	3:1	20
Normal vs. lazy (ageotropic)	la	la	3:1	21
Erect vs. prostrate growth	la	Er	3:1	62, 70
Erect vs. spreading vs. prostrate growth.			1:2:1	82
Spreading (decumbent habit) vs. erect.	er	Es	3:1	36, 62
Normal vs. deep water paddy (floating habit).	dw	ef_1, ef_2	15:1	72

Table 1. Continued

Characters	Symbols		Segregation ratios	Author reporting segregation[2]
	Recommended	Kadam & Ramiah proposal		
D. Physiologic and disease,				
Scented (aromatic vs. non-scented grain.	Sk	Oa, Ob, Oc	3:1, 9:7, 27:37	29
Late vs. early flowering	Lf	fl_1, fl_2, fla, flb	3:1, 15:1, 9:7	1, 4, 12, 17, 19, 20, 22, 38, 51, 52, 75, 77
Early vs. late flowering	Ef	Ifl	3:1, 1:2:1	64, 66, 67
Fertile vs. sterile (various types).	s	fan, fb, fo, fm, fp	3:1	3, 15, 16, 23, 31, 34, 39, 45, 46, 61, 79
Normal vs. albino	al	w_1, w_2, w_3	3:1, 9:7, 15:1, 63:1	7, 27, 28, 40, 41, 62
Normal vs. chlorina	chl	chl	3:1	39, 41, 71
Normal vs. yellow	y		3:1, 15:1	32, 33, 71
Normal vs. lutescent	lu	l	3:1	71
Normal vs. lethal yellow	l-y	y_1, y_2	3:1, 15:1	27, 35, 40, 41, 62, 71
Normal vs. tipburn yellow	tb	tp_{al}, tp_b	9:7	27
Normal vs. very elongated yellow			3:1	14
Normal vs. variegated	var	vr	3:1	37, 48, 55
Normal vs. variegated vs. albino			9:3:4	71
Normal vs. virescent vs. albino			9:3:4	71
Normal vs. virescent vs. variegated.			9:3:4	71
Normal vs. virescent yellow vs. virescent white.	v	v_1, v_5, vj_1	9:3:4, 9:7, 45:15:4, 45:9:10	24, 27
Normal vs. virescent stripe vs. virescent white vs. albino.	al		9:3:3:1	27
Green vs. xantha			3:1	71
Cercospora resistance vs. susceptibility.	ce	ce_1	3:1	1, 73
Sclerotium oryzae resistance vs. susceptibility.	Sc	le	3:1	Kato 1916[4]
Blast resistance vs. susceptibility.	Pi	pia_1, pib	3:1, 9:7	49, 74
Lodging vs. non-lodging	Ld	ld	3:1	4, 68

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Other Than Anthocyanin Colors, as Reported Before 1943[5]

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Table 2. Inheritance of genetic characters in rice reported from India prior to 1943, relating to the symbolization summarized by Ramiah and Rao in their 1953 study, Rice Breeding and Genetics,[1] and to a recommended symbolization

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
A. Anthocyanin color				
a. Awn				
Red vs. white			3:1	8
Purple vs. white			3:1	51
b. Apiculus --	CAP			
Purple vs. colorless			3:1	9, 24, 28,
Do.			9:7	9, 24
Do.			15:1	9
Do.			27:37	9
c. Hull (lemma and palea) --	Pr			
Dark purple vs. tawny	Pr	A c Hp vs.	3:1	35 (1934)
Purple vs. non-purple (from green x tawny)		A c Ht	9:7	35 (1936)
Colored vs. green (from green x green)			9:7	9, 24, 28
Full purple vs. green			3:1	24, 28
Purple vs. purple tip vs. green (from green x green)	Pr	Hep_1, Hep_2	9:3:4	*
Purple vs. purple and patchy gold vs. green vs. gold.			9:3:3:1	*
d. Outer glumes				
Purple vs. green	Pg		3:1	9, 24, 35 (1932)
Purple vs. green (from green x green)			9:7	9

[1] Table is an adaptation from: Ramiah, K., and Rao, M. B. V. N. (1953). Rice breeding and genetics. Sci. Monog. Indian Council Agr. Res. 19, 360 pp.

[2] Numbers refer to a list of references following this table. The references are part of the bibliography of the above publication.

*Unpublished record of Paddy Breeding Station, Coimbatore.

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
e. Stigma --	Ps			
Purple vs. colorless			3:1	9, 24, 29
Do.			9:7	24
Do.			27:37	9
Do.			81:175	9
f. Coleoptile				
Colored vs. colorless			3:1	Chakravarty (unpub)
g. Leaf blade --	Pl			
Purple vs. green			3:1	28
Do.			9:7	28, 48 (1934)
Do.	Pl, I-Pl	Lp, Ilp	3:13	4 (1938), 11
Do.			15:1	Ramiah (unpub)
Green vs. purple			3:1	4 (1938)
Intermediate vs. full purple vs. green			39:9:16	1 (1938)
Full purple vs. partial vs. margin vs. green	Pl, Pla?	P_1, P_2, P_3	9:39:12:4	Ramiah (unpub)
Full purple vs. margin vs. green			12:3:1	Ramiah (unpub)
Purple margin vs. green			3:1	20
h. Collar (junctura)				
Colored vs. colorless			3:1	28
i. Auricle				
Colored vs. colorless			3:1	18, 24
Do.			9:7	9, 20
j. Ligule --	Plg			
Purple vs. white	Plg	Lgp (AC)	3:1	9, 18, 20, 24, Ramiah (unpub)
Do.	Plg	Lgp (AC)	15:1	Ramiah (unpub)
Do.			9:7	9, 24
Do.			27:37	9, 24

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
k. Sheath --	Psh			
Colored vs. colorless			3:1, 9:7, 27:37, 15:1	9, 24, 28
Purple lines vs. green	Psh	Lsn	3:1	*
Self purple with lines vs. self vs. lines vs. green.			9:3:3:1	*
Normal vs. striping			3:1	27
l. Pulvinus --	Pu			
Purple vs. green			3:1	20, 28
Do.			9:7	9, 24
m. Axil --	Px			
Dark purple vs. light purple			3:1	*
n. Stem node --	Pn			
Purple vs. green			3:1	20
o. Septum				
Purple vs. yellow vs. brown			9:3:4	5
Dark purple vs. pink			3:1	*
Dark purple vs. light purple vs. green			9:6:1	*
p. Internode --	Pin			
Colored vs. colorless			3:1	9, 24
Do.			27:37	9
Self purple vs. lines			3:1	*
Self purple vs. lines vs. light lines vs. green			9:3:3:1	*
Purple lines vs. medium dark lines vs. very dark lines.	Pin	A, B	12:3:1	*
Light purple vs. green vs. light brown (from green x purple).			9:3:4	24
Light purple vs. green vs. light brown (from green x light brown).			9:3:4	24

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
q. Root				
Red vs. white			9:7	14
r. Kernel				
Red vs. white (from white x white).	RcRd		9:7	24
Light red vs. faint red vs. white.	Rc		1:2:1	1 (1940)
Light red vs. white	Rc		3:1	1 (1940), 10
Dark red vs. light red			9:7	10
Red vs. white	Rc		3:1	7, 10, 19
Do.	RcRd		15:1	42
Red vs. amber vs. white	RcRd		12:3:1	20
Full red vs. gray brown vs. white.	RcRd		9:3:4	29
Purple vs. white	Prp		3:1	24, 29
Purple vs. red vs. white (from purple x red).	PrpRc		12:3:1	29
Purple vs. red vs. white	PrpRc	Prp, Pr	12:3:1	Ramiah (unpub)
Red (Gh) vs. white (Gh) vs. gold (gh) vs. white (gh).	RcGh		9:3:3:1	M. B. V. Narasinga Rao (unpub)
B. Other colors of lemma and palea				
a. Green stage				
Green vs. dark brown furrows	H^f	H, H^f	3:1	4 (1937), 9, 22, 28, 35 (1935)
Green vs. dark brown furrows	I-H^f, H^f		13:3	19
Dark brown furrows vs. dark gold.	H^f		3:1	9, 29
Green vs. black vs. light gold vs. dark gold.			9:3:3:1	22
Green vs. intermediate vs. dark gold.			9:6:1	24

Table 2. Continued

Characters	Symbols		Segragation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
b. Ripe stage				
Black vs. straw	Bh		3:1, 9:7	29
Black vs. yellow vs. blackish brown (from black furrows x straw).	Bh, H^f, Gh		36:21:7	22, 25
Black vs. straw vs. dark furrows vs. brown.	Bh, H^f		9:3:3:1	10
Piebald black vs. piebald straw vs. black with "dirty" furrow vs. straw with "dirty" furrow.	Bh, H^i vs. H^p		9:3:3:1	*
Black vs. non-black (from black x gold).	Bh		3:1	10
Green ripening black vs. green ripening straw vs. gold ripening black vs. gold ripening straw.	Bh, Gh		9:3:3:1	Berhampore Rice Res. Sta. (unpub).
Straw vs. gold	Gh		3:1	24, 28, 48 (1938)
Green vs. gold internode (pleiotropic).	Gh		3:1	28
Straw vs. yellow vs. dark gold.			9:6:1	9
Piebald furrows vs. dark furrow vs. piebald gold vs. dark gold.			9:3:3:1	28
Piebald furrows vs. straw			3:1	28
"Dirty" furrows vs. intermediate vs. mottled.			1:2:1	34
Mottled vs. unmottled (from piebald x mottled "dirty").	H^m	H^m	3:1	34

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
C. Presence of structures				
a. Pubescent vs. glabrous (smooth)	gl	Lh = A_{na}, A_{nb}	3:1	35 (1936)
Do.			15:1	48 (1937)
b. Awned vs. awnless	An		3:1	Ramiah (unpub)
Do.	An	A_{n_a}, A_{n_b}	9:7	6 (1935), 35(1935)
Do.	An	A_{n_1}, A_{n_2}	15:1	20, Ramiah (unpub)
c. Awned vs. slightly awned vs. awnless	An		9:6:1	19, Ramiah (unpub)
d. Awned vs. partly awned vs. awnless	An		12:3:1	Ramiah (unpub)
e. Awned of all degrees vs. awnless	An	A_{n_1}, A_{n_2}, A_{n_3}	63:1	51, Ramiah (unpub)
f. Tillering			Quantitative	3, 42,*
D. Size and shape				
a. Spikelet and grain				
1. Length			Quantitative	3, 19
Normal vs. short round			3:1	28
Short round vs. long	Rk		3:1	41
Short vs. long	lk		3:1	23
Shortness dominant in Indica x Japonica			Quantitative	6 (1935)
Short vs. medium length	lk		3:1	1 (1939)
Short vs. medium			9:7	1 (1939)
Short vs. very short			3:1	4 (1939)
Short vs. very short vs. medium (from very short x medium).			9:6:1	4 (1939)
Medium vs. short			3:1	4 (1939)
Long vs. medium			3:1	4 (1939)
No dominance from short x long			Quantitative	4 (1939)
2. Breadth			Quantitative	23, 44
Medium vs. coarse			3:1	4 (1939)
Medium vs. fine			3:1	4 (1939)
3. Thickness			Quantitative	19
Round (from round x ordinary)			Dominant	19
b. Glumes				
Normal vs. long outer glumes	g		3:1	28
Normal vs. intermediate vs. long	g		1:2:1	41

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
c. Short anther (wild x cultivated)			Dominant	Berhampore Rice Res. Sta. (unpub).
d. Panicle length			Quantitative	3, 6 (1935), 33
e. Height --	T			
Tall vs. short			3:1	37
Short vs. tall	T, I-T?	T_1, T_2	3:1	37
f. Leaf width				
Normal vs. narrow (from X_2 progeny)	nal	In	3:1	46
Broad vs. narrow			3:1	6 (1935)
g. Dwarfing --	d			
Normal vs. dwarf			3:1	13, 29
Normal vs. stumpy (from X_2 progeny)			3:1	46
E. Modified structure				
a. Spikelet				
Normal vs. multiple pistil	mp		3:1	30
Shattering vs. non-shattering	Sh	sh	3:1	39
Do.	Sh		15:1	12
Shattering partially dominant			Quantitative	48 (1933)
Shattering			Quantitative	2
b. Panicle				
Well exserted vs. partially exserted			Quantitative	35 (1932)
Exserted and mostly exserted vs. tip exserted vs. enclosed.	Ex		49:3:12	50
Cluster vs. intermediate vs. non-cluster	Cl	cl	1:2:1	41, 48 (1936)
Cluster vs. normal	Cl		63:1	Kadam (unpub)
Lax vs. dense	Lx	Lx	3:1	3, 6 (1935), 20, 33
Lax vs. cigar shaped (dense?)	Lx		3:1	29
c. Leaf				
Normal vs. rolled leaf	rl	lro_1, lro_2	15:1	46
Normal vs. twisted	tl		3:1	15

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
d. Stem				
Bent node vs. straight	Bn	Nb_a, Nb_b	9:7	*
Lodging vs. non-lodging	Ld		3:1	43
Lodging dominant			Complex	3
F. Modified composition				
a. Soft vs. intermediate vs. hard endosperm			1:2:1	10
b. Translucent vs. abdominal white vs. opaque			1:2:1	6 (1938)
c. Abdominal white vs. translucent			3:1 (Xenia)	4 (1939)
d. Starchy vs. waxy (glutinous)	wx	Wx	3:1 (Xenia)	6 (1936), 29, 41
e. Scented (aromatic) vs. non-scented endosperm	Sk		3:1, 9:7	38
Do.	Sk		27:37	17
Do.	Sk		3:1 (Xenia)	4 (1940)
Do.	Sk		3:1, 15:1	53 (1941)
G. Modified growth habit				
a. Normal vs. ageotropic	la	la	3:1	45
b. Spreading vs. compact (erect)	er	Es	3:1	33
c. Procumbent vs. compact (erect)	er	Er	3:1	33
d. Normal vs. floating	dw	ef_1, ef_2	15:1	40
H. Physiologic				
a. Sterility --	s			
Normal vs. sterile stiff panicle (X_2 progeny)			3:1	46
Normal vs. sterile			Complex	48 (1936)
Normal vs. sterile (from Indian x American)			Complex	6 (1938)
Normal vs. "spongy," i.e.sterile, tip (X_2 progeny)	s		3:1	46
Normal vs. barren (X_2 progeny)	s		15:1	46
Normal vs. asynaptic	s		9:7	32
Normal vs. male sterile	s		3:1	31, 53 (1938)
b. Photoperiodic response --			Quantitative	1 (1939), 6 (1936)
Early vs. late	Ef		3:1	9
Late vs. early	Lf		3:1	6 (1936)
(Early x early)			Quantitative	36
Late vs. early	Lf		3:1	49

Table 2. Continued

Characters	Symbols		Segregation ratios	Author reporting[2]
	Recommended	Of indicated author(s)		
Late vs. early			Quantitative	52
Early vs. late (from early summer x winter rice)	Ef		3:1	26
Late vs. early (from early summer x autumn rice)			Quantitative	26
Late vs. early (from autumn x winter rice)	Lf		3:1 (transgressive)	26
Late vs. early	Lf		3:1	40
Non-sensitive vs. sensitive	Se		3:1	53 (1937)[3]
c. Chlorophyll deficiencies				
1. Lethal				
Normal vs. albino	al		15:1	16,33
Do. (from segregating families)	al		3:1, 15:1	47
Normal vs. albino with yellow coleoptile (X_2 progeny).			3:1, 15:1	46
Normal vs. yellow (xantha)			3:1, 15:1	15, 47
Normal vs. lutescent	lu	l	3:1	47
Normal vs. virescent yellow vs. albino (from albino x virescent yellow).			9:3:4	47
Normal vs. green and white stripe vs. albino (from albino x green and white stripe).			9:3:4	47
Normal vs. striped vs. albino	al	W, G	12:3:1	21
2. Non-lethal				
Normal vs. tipburn yellow	tb	tp_a, tp_b	9:7	15
Normal vs. virescent yellow	v	v	3:1, 15:1	33
Normal vs. green and white stripe	fs		3:1	21, 27, 47
Normal vs. virescent yellow vs. green and white or white and yellow stripe.			9:3:4	47
Normal vs. yellow and white stripe			15:1	47
Normal vs. zebra (yellow band)	z	zy	3:1	46
Normal vs. zebra (white band)	z	zw	3:1	46
Normal vs. blotched white			3:1	46

[3] Also, Chandraratna, M. F. (1953). A gene for photoperiod sensitivity in rice linked with apiculus colour. Nature 171: 1162-1163.

Articles on Inheritance and Symbolization of Genetic Characters in Rice as Reported (Entirely From India) Before 1943[6]

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Table 3. Inheritance of genetic characters in rice reported from India since about 1950, relating to the symbolization given by various authors[1] and to a recommended symbolization

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
A. Anthocyanin color				
a. Coleoptile				
Purple vs. green	Pl	Cp_1, Cp_2 (AC)	9:7, 27:37, 45:19, 54:10, 162:94	8
Nonpigmented vs. pigmented	Pl, I-Pl	ICp_1, ICp_2	13:3, 15:1, 229:27	8
b. Leaf sheath --	Psh			
Coloured vs. green	Psh	Lsp_1 Lsp_2 (AC)	3:1, 9:7, 27:37, 45:19, 81:175, 162:94	8
Purple vs. dark purple vs. green			9:3:4	3
Purple vs. non-purple			9:7, 45:19, 54:10, 117:139, 27:9:28	9
c. Leaf blade --	Pl			
Green vs. purple	Pl, I-Pl	L, l-L, l-L	13:3, 57:7	2
Green vs. purple	Pl, I-Pl		3:1, 13:3	3
Green vs. purple	I-Pl	lpl, Lp (AC)	13:3, 55:9, 229:27	7
Purplewash vs. green	Pw	Lpw, Ld (AC)	9:7, 27:37	7
Purplewash vs. faint purplewash vs. green (from faint purplewash x green).	Pw	*Lpw, Ld or L'd (AC)	27:9:28	7
Purplewash vs. purple vs. green (from purple x purplewash).	Pw	Lp, Lpw, lpl (AC)	39:12:13	7
Purplewash vs. faint purplewash	Pw	Ld vs. L'd	3:1	7
Purple vs. non-purple	Pl		9:55, 27:37, 27:229, 81:175	9

[1] None of the authors here reviewed were cited by Ramiah and Rao in their 1953 study, Rice Breeding and Genetics; their latest citation was to a 1942 work. (See table 2.)

[2] Symbols for basic genes are in parentheses. [3] Numbers refer to a list of references following this table.

*Ld and L'd are alleles complementary to Lpw; Lpw-Ld = purplewash, Lpw-L'd = faint purplewash. These genes do not modify Lp, nor does lpl modify Lpw.

Table 3. Continued

Characters	Symbols		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
d. Leaf tip and margin --	Pla			
Purple vs. green			27:37	4
Purple vs. non-purple			9:55, 45:19, 27:229, 81:175	9
e. Auricle				
Dark purple vs. white			9:7	3
Purple vs. green	Plg?	Aup_1, Aup_2 (AC)	3:1, 9:7, 54:10, 162:94	8
Purple vs. non-purple			45:19, 27:229, 81:175	9
f. Ligule --	Plg			
Pigmented vs. nonpigmented	Plg	Lgp_1, Lgp_2 (AC)	3:1, 9:7, 54:10, 45:19, 162:94	8
Purple vs. non-purple			27:37, 45:19, 27:229	9
g. Junctura (i.e. collar)				
Purple vs. green	Plg?	Jp_1, Jp_2 (AC), I-Jp, Al-Jp	3:1, 9:7, 15:1, 45:19, 54:10, 117:139, 162:94	8
Purple vs. non-purple			45:19, 162:94, 81:175	9
h. Junctura back				
Purple vs. green	Plg?	Jp_1, Jp_2 (AC)	9:7, 27:37, 45:19, 54:10, 162:94	8
Purple vs. non-purple			9:7, 27:37, 45:19, 27:229	9
i. Pulvinus --	Pu			
Purple vs. green	Pu	Pup_1, Pup_2, Pup_3 (AC)	3:1, 9:7, 54:10, 162:94, 243:781	8
Purple vs. non-purple			27:37, 45:19, 81:175	9
j. Internode --	Pin			
Purple vs. green	Pin	Ntp_1, Ntp_2 (AC), I-Ntp, AI-Ntp	9:7, 27:37, 81:175, 117:139, 162:94	8
Purple vs. non-purple	Pin		9:7, 45:19, 54:10, 162:94	9
k. Septum				
Pigmented vs. nonpigmented			9:7	1
Purple vs. non-purple			3:1, 45:19	9

Table 3. Continued

Characters	Symbols		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
l. Leaf axil --	Px			
Colored vs. colorless	Px	Lxp_1, Lxp_2 (AC)	3:1, 9:7, 27:37, 54:10, 45:19, 81:175, 162:94	8
Purple vs. non-purple	Px		9:7, 45:19, 81:175	9
m. Apiculus --	CAP			
Purple vs. green	CAP	Ap_1, Ap_2, Ap_3 (AC)	3:1, 9:7, 15:1, 27:37, 45:19, 54:10, 162:94	8
Purple vs. non-purple			3:1, 9:7, 27:37, 45:19, 81:175	9
n. Glumes (outer glumes)				
Colored vs. colorless	Pg	Gp_1, Gp_2, Gp_3 (AC)	3:1, 9:7, 27:37, 81:175, 117:139, 243:781	8
Purple vs. green		I-Gp, Al-Gp	3:1, 9:7	9
o. Lemma and Palea				
Purple vs. green			3:1, 9:55, 27:229	9
p. Stigma --	Ps			
Purple vs. white	Ps	Sp_1, Sp_2 (AC)	3:1, 9:7, 27:37, 45:19, 81:175, 162:94	8
Purple vs. non-purple			3:1, 45:19, 81:175	9
q. Pericarp --	Prp			
Purple vs. brown vs. white			9:3:4	5
B. Other colors				
a. Lemma and palea				
Straw vs. piebald brown vs. brown furrows vs. brown.			9:3:3:1	3
C. Presence of structures				
Normal vs. rudimentary auricle			3:1	5
Normal vs. auricleless	lg	au_1, au_2, au_3, au_4	255:1	6
Normal vs. liguleless	lg	lg_1, lg_2, lg_3, lg_4	255:1	6

Table 3. Continued

Characters	Symbols		Segregation ratios	Author reporting[3]
	Recommended	Of Indicated author(s)		
Normal vs. juncturaless	lg	J_1, J_2, J_3, J_4	255:1	6
Normal vs. auricleless, liguleless, juncturaless.	lg		3:1	1
Normal vs. auricleless, liguleless, juncturaless.	lg		15:1	9
Awned vs. awnless	An		54:10	1
Awned vs. awnless	An		9:7, 27:37, 81:175, 243:781	8
Awned vs. awnless	An		3:1, 15:1, 27:37, 54:10	9
Unnotched vs. notched	Nk, I-Nk	Nk, INK	13:3	5
Hairiness vs. glabrous (hull)	gl		3:1	11
Very hairy vs. ordinary	Lh	Lh_1, Lh_2, Lh_3, Lh_4	3:1, 9:7, 162:94	10
Normal vs. long glume	g	g_1, g_2, g_3	3:1, 54:10	10
Beaked lemma vs. normal	Bd	Hbd_1, Hbd_2	3:1, 9:7	10
D. Size				
Normal vs. dwarf	d		3:1, 15:1, 54:10	1
Short vs. very short kernels	rk		3:1	3
Medium vs. short			3:1	3
E. Modified structure				
Normal vs. presence of fleshy structure			3:1	5
Dense panicle vs. lax panicle	Dn		9:7	2
Normal vs. multiple pistil	mp	mp	3:1	2, 3, 5
Clustered (including intermediate vs. normal).	Cl		3:1	10
Normal (single and intermediate) vs. clustered.			3:1	10
F. Modified composition				
Endosperm				
White vs. translucent			3:1	3

Table 3. Continued

Characters	Symbols		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
G. Physiologic				
Spreading growth vs. erect	er		3:1	3
Non-scented vs. scented	I-Sk?		3:1	3, 5
Absence of aroma vs. presence of aroma	Sk, I-Sk		13:3	2
Medium ripening vs. early ripening			3:1	3
Normal vs. albino	al	w_1, w_2, w_3, w_4	3:1, 15:1, 255:1	8
Normal vs. xantha	l-y	Y_1, Y_2	3:1, 15:1	8

Articles on Inheritance and Symbolization of Genetic Characters in Rice as Reported (Entirely From India) Since About 1950

1. Bhattacharya, R. K. (1957). Genetics of rice (Oryza sativa L.). Inheritance of anthocyanin pigmentation and other morphological characters in inter varietal crosses within Indica group. Unpublished thesis for the associateship of the Indian Agricultural Research Institute.

2. Chakravorty, A. K. (1948). A genetical study of botanical characters in rice, Oryza sativa L. Bul. Bot. Soc. Bengal 2: 50-58.

3. Dave, S. B. B. (1948). Inheritance of characters in Central Provinces' rices. Nagpur [India] Agr. Col. Mag. 23: 20-50.

4. Dubey, S. N. (1955). Studies on the inheritance of anthocyanin pigmentation in inter racial crosses in rice (Oryza sativa L.). Unpublished thesis for the associateship of the Indian Agricultural Research Institute.

5. Ghose, R. L. M., and Butany, W. T. (1952). Studies on the inheritance of some characters in rice (Oryza sativa L.). Indian J. Genet. & Plant Breed. 12: 25-30.

6. Ghose, R. L. M., Butany, W. T., and Seetharaman, R. (1957). Inheritance of ligule, auricle and junctura in rice (Oryza sativa L.). Indian J. Genet. & Plant Breed. 17: 96-101.

7. Ghose, R. L. M., Butany, W. T., and Seetharaman, R. ( ). Inheritance of anthocyanin pigmentation in leaf blade of rice (Oryza sativa L.). Indian J. Genet. & Plant Breed. (In press.)

8. Ghose, R. L. M., Ghatge, M. B., and Subrahmanyan, V. (1956). Rice in India. New Delhi. India: Indian Council of Agricultural Research, 507 pp.

9. Iyer, K. N. (1959). Genetics of rice (Oryza sativa L.). The inheritance of awning, auricle, ligule and junctura and anthocyanin pigmentation and the interrelationship of genes governing these characters. Unpublished thesis for the associateship of the Indian Agricultural Research Institute.

10. Rajappan Nair, N. (1958). Genetics of rice (Oryza sativa L.). The inheritance of hairiness, clustering, beaked habit, anthocyanin pigmentation and the interrelationship of genes governing these characters. Unpublished thesis for the associateship of the Indian Agricultural Research Institute.

11. Sampath, S., and Seshu, D. V. (1958). Glabrousness in rice. Rice News Teller 6 (2): 13-14.

Table 4. Inheritance of genetic characters in rice reported from Japan since about 1940, relating to the symbolization given by various authors[1] and to a recommended symbolization

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
A. Anthocyanin and related colors				
a. Basic				
Chromogen (tawny or colorless).	C^BC^Bp, $C^{Bt}C^{Br}$, c	C	3:1	11, 30, 33, 35, 41, 43, 46, 61, 85
*Enhancer of C (see P)	En-C_d	P	3:1	30
Activator (partial purple or red).	A, A^d, a (C)	Sp, A, or Ap	3:1	30, 35, 41, 43, 45, 46, 47, 53, 61, 85
b. Apiculus				
Fully colored vs. colorless.	P (CA)	A, Ap, or C	3:1, 9:7, 27:37	4, 11, 32, 33, 58, 85
Purple vs. white (shades depend on combinations of alleles).	CA (P?)		3:1 (9:7)	32, 33
Red vs. white (shades depend on combinations of alleles).	CA (P?)		3:1 (9:7)	30
Tawny vs. straw	C	Ty or C	3:1	4, 11, 35, 36, 41, 43, 46, 53, 61, 85
c. Hull (lemma and palea)				
*Colored vs. colorless	Pr (CA)	Rp or Pal	3:1 (9:7, 27:37)	30, 32, 35, 36, 41, 43, 46, 85
d. Stigma				
Colored vs. colorless	Ps (CA) or P (CA)	Ps or A	3:1, 9:7 (27:37, 45:19, 180:76)	11, 58, 86

[1] Authors here reviewed are in general supplemental, in the sense of updating, to those cited by Kadam and Ramiah in their 1943 study, Symbolization of Genes in Rice. However, 9 citations supplement those of Kadam and Ramiah for the period 1941-42. One of these 9 citations is found in Kadam and Ramiah--with reference to a different character (see table 1, citation 43). A 1926 citation in Kadam and Ramiah is repeated as an addition regarding rice sterility (see table 1, citation 16).

[2] Symbols for basic genes are in parentheses. [3] Numbers refer to a list of reference following this table.

*Genes apparently not reported from U. S. A.

Table 4. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
e. Leaf				
Colored vs. colorless	Pl (CA)	Pl or R	3:1 (9:7, 27:37)	4, 30, 32, 35, 43, 46, 49, 51, 85
Colored vs. colorless		Additional gene	81:175	92
Colorless vs. colored	I-Pl	I-pl	3:1 (13:3)	49, 51, 85
f. Node				
*Colored vs. colorless	Pn (CA)	Pn	3:1 (9:7, 57:7, 1:1)	35, 48, 50, 85
B. Other colors				
a. Pericarp				
Brown vs. normal	Rc	Rc	3:1	35, 43, 69
Red vs. non-red	Rd (Rc)	Rd or Aer	3:1 (9:7)	4, 5, 35, 43, 46
b. Hull				
*Dark (brown) furrows vs. straw color	Bf	F	3:1	55, 56
Straw color vs. dark furrows	I-Bf	If or fd	3:1 (13:3)	43, 55, 56
Straw color vs. goldhull	gh	rg	3:1	55, 56
*Blackhull vs. normal straw color	Bh_a, Bh_b, Bh_c	Rb_1, Rb_2, Rb_3 or cr, Kb, Ax	9:7, 27:37	4, 55, 56
C. Presence of structures				
Awned vs. awnless	An_1, An_2, An_3	An_1, An_2, An_3 or Ar_1, Ar_2, Ar_3	3:1, 15:1, 63:1	4, 37
Normal vs. liguleless	lg	lg	3:1	28, 32, 52
Pubescent vs. glabrous	gl	gb	3:1	59
D. Size				
a. Grain				
Length			Quantitative	5

Table 4. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
Length			Quantitative	29
Length, breadth and width		Gr_1, Gr_2, Gr_3	Quantitative	75, 77
Short vs. long empty glumes	g	lng	3:1	28, 35
b. Panicle and stem				
*Panicle length		P_1, P_2, P_3, P_4, P_5	Quantitative	71, 73, 74, 82
Stem length		H_1, H_2, H_3	Quantitative	72, 83
c. Dwarf				
Normal vs. daikoku (thickset).	d_1, d_8	d_1, d_8	3:1, 15:1	28, 39, 42, 54, 65, 66
Normal vs. ebisu (moderately thickset).	d_2	d_2	3:1	39, 42, 59, 66
Normal vs. tillering	d_3, d_4, d_5	d_3, d_4, d_5	3:1, 15:1, 63:1	28, 39, 42, 35, 59
Normal vs. lop-leaved	d^3_6	d_6	3:1	42, 59
Normal vs. cleistogamous	d_7	d^6_7	3:1	57
Normal vs. very small	d		3:1	31
Normal vs. sohtoku-1 (depressed awns)	d_s		3:1	28
Normal vs. tankan-shirasasa (sinuous neck).	d_t		3:1	28
Normal vs. bonsai (rolled leaf).	d_b or rl?		3:1	28
Normal vs. waisei-shirasasa (twisted leaf).	d_w		3:1	28
Normal vs. compact panicle.	d_c		3:1	28
Normal vs. Kojo-tamanishiki (slender).	d_k		3:1	28

Table 4. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
E. Modified structure				
a. Spikelet				
*Normal vs. cleistogamous spikelets.	cls	cls	3:1	57
Low vs. high shattering of grains.	Th	sh	3:1	15, 59
*Normal vs. poly-embryonic (multiple embryos).	me_1, me_2	a, b	15:1	16
*Normal vs. poly-caryoptic (multiple pistils).	mp		3:1	34
*Normal vs. depressed palea.	dp_1	pa	3:1	30, 32
*Normal vs. under-developed palea.	dp_2	Gl	3:1	74
*Normal vs. claw-shaped hull.	clw		3:1	84
*Normal vs. triangular hull.	tri		3:1	28
*Normal vs. notched grain	nl		3:1	28
b. Leaf				
*Normal water repellent vs. glossy[4].			3:1	28
c. Panicle				
*Undulate vs. normal rachis.	Ur	Ur	1:2:1	59, 61
*Dense vs. normal	Dn	Dn	3:1, 1:2:1	59, 61
Dense vs. normal	Dn^1	Ka	1:2:1	73, 75
Normal vs. lax	Dn^2	lax	3:1	28, 30, 32
*Normal vs. lax with large grains.	^{3}		3:1	28
Normal exerted vs. enclosed.	Ex		3:1	28
Normal vs. neck leaf	nl	hk	3:1	59

[4] Water spreads over surface; observable on glabrous leaf only.

Table 4. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
d. Stem				
Procumbent (spreading) vs. erect growth.	er	Pros	3:1	4
Normal vs. lazy (spreading growth).	la	sg	3:1	28, 35, 59
F. Modified composition				
Vitreous vs. waxy (glutinous) endosperm.	wx	gl or m	3:1	36, 38, 85
Normal vs. brittle culm	bc	bc	3:1	59
G. Physiologic				
a. Sterility --	s			
Normal vs. male sterile	s_1	sf	3:1	10, 11
Normal vs. male sterile	s_2	sk	3:1	10, 11
Normal vs. compact paniclous sterile.	s_3	cps	3:1	84, 87
Normal vs. partial sterile			7:1	14
*Gamete-development genes		S_1, S_2, T_1, T_2	Quantitative	68
b. Photoperiodic response				
Late vs. early flowering	Lf_z	Z	1:2:1	1
Do.	Lf_m	M	1:2:1	1, 3
Do.	Lf_k	K	1:2:1	1, 2
Do.	Lf_g	G	3:1	1
Do.	Lf_o	O	3:1	1, 3
Do.	Lf_f	F	3:1	1
Do.	Lf_1, Lf_2	E_1, E_2		22, 24
Do.	Lf_3, Lf_4, Lf_5	E_3, E_4, E_5		78, 80, 81
Do.	Lf_a, Lf_b,	E_a, F_b		79
Early vs. late flowering	Ef_1, Ef_2	Fl, Se	3:1, 15:1	91

Table 4. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
c. Chlorophyll deficiencies				
Normal vs. albino	al_1	al	3:1	6, 9
Do.	al_2	al	3:1	84
Normal vs. striped	v	gw	3:1	84
*Normal vs. fine stripe margin	fs	fs	3:1	84
Normal vs. variegated			Maternal(3 strains)	17, 18, 19, 20, 21
Normal vs. chlorina	chl_1	ch_I	3:1	6
Do.	chl_2	ch_{II}	3:1	6
Do.	chl_3	ch_{III}	3:1	6
Do.	chl_4	ch_{IV}	3:1	6, 7
Do.	chl		3:1	19, 20, 21
Normal vs. xantha	xa_1, xa_2	Xa_I, Xa_{II}	3:1, 15:1	6
Do.	xa_3	Xa_{III}	3:1	8
Do.	xa_4	Xa_{IV}	3:1	8
d. Disease				
Resistance vs. susceptibility to:				
Piricularia oryzae	Pi_1, Pi_2		3:1, 15:1, 9:3, 3:1	12
Piricularia oryzae	Pi	Bt	One major gene	70
*Resistance vs. susceptibility to:				
Sclerotium oryzae	Sc_1, Sc_2		3:1, 15:1	13

Table 4. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
Normal vs. mottled leaf	bl	mg or mt	3:1	28, 55, 56
H. Miscellaneous				
*Positive vs. negative phenol staining.	Ph	Ph	3:1	24, 52, 59, 69
*Positive vs. negative iodine-potassium iodide staining.			Quantitative	40

Articles on Inheritance and Symbolization of Genetic Characters in Rice as Reported (Entirely From Japan) Since About 1940

(The references, with indicated exceptions, are entirely in Japanese.)

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TABLE 5. Inheritance of genetic characters in rice reported from the United States since about 1940, relating to the symbolization given by various authors[1] and to a recommended symbolization

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
A. Anthocyanin color				
Purple apiculus vs. colorless	CAP	Ap, Ap_a, Ap_b	3:1, 9:7, 27:37	2, 5, 8, 10
Colored hull furrow vs. colorless		Hft	9:7	10
Purple lemma and palea vs. light purple apiculus	Pr (CAP)?		27:37	5, 7
Purple lemma and palea vs. purple apiculus and apex	Pr (CAP)?		27:37	5, 7
Purplehull vs. colorless	Pr (CAP)?	Hp	3:1, 9:7	2, 8
Purple outer glumes vs. colorless			3:1	5, 7
Purple collar vs. colorless			3:1	5
Purple vs. green sheath			3:1	4
Purple plant (leaf) vs. colorless	Pl	Pl	9:7	10
Purple vs. colorless pericarp	Prp	Prp	3:1, 9:7	2, 8
Brown vs. ordinary pericarp	Rc		3:1	4
Red vs. colorless	Rd (Rc)	Pr	3:1	2, 8
B. Other colors				
Straw vs. goldhull (golden yellow)	gh	hg	3:1	2, 3, 4, 5, 7, 8, 10
Whitehull vs. normal strawhull (epistatic to Gh; with gh produces yellowhull).	Wh	Hw	3:1	8
C. Presence of structures				
Awnless vs. awned	An, I-An		3:1, 13:3	2, 4, 8
Pubescent vs. glabrous (hairiness)	gl	lh	3:1	2, 3, 5, 7, 8, 10
Normal vs. long extra lemma	lmx	lmx	3:1	8
*Normal vs. neck leaf	nl		3:1	8, 12
Normal vs. liguleless	lg	lg	3:1	8
D. Size				
Normal vs. thickset dwarf	d		3:1	9
Normal vs. grassy dwarf	d		3:1	9
Normal vs. crinkleleaf dwarf	d	dx	3:1	8

TABLE 5. Continued

Characters	Symbols[2]		Segregation ratios	Author reporting[3]
	Recommended	Of indicated author(s)		
*Normal vs. short small seed (X-ray mutation)	d		3:1	12
Normal vs. long glumes	g	g	3:1	2, 8
Partially dominant long glume vs. normal (epistatic to g)	Gm	Gl	3:1	8
E. Modified structure				
Clustered vs. non-clustered (arrangement of spikelets)		Cl	3:1	6, 8
*Normal vs. compact panicle			3:1	12
*Normal vs. enclosed panicle, Sathi type	Ex		1:2:1	12
*Normal vs. coarse culm (big in diameter)	bg		3:1	12
*Normal vs. rolled leaf (dwarf type, partially sterile)	rl		3:1	12
F. Modified composition				
Vitreous vs. large chalky core (soft starch)	wc		9:7	4
Vitreous vs. waxy (glutinous)	wx	wx	3:1	8, 10
Normal vs. brittle culm	bc	bc	3:1	8
G. Physiologic				
*Normal vs. hull spots	hsp		3:1	12
*Normal vs. haploid 3 (dwarf sterile)	s		3:1	12
*Normal vs. compact sterile (X-ray mutation)	s		3:1	12
Fragrant vs. non-fragrant flower	Fgr	Fgr	3:1	7
Late vs. early flowering	Lf		3:1	1, 7
Normal vs. virescent leaves	v	v	3:1	6
Normal vs. albino and striped	al		15:1?	4
H. Disease				
*Normal vs. physiologic disease I (discoloration of entire plant).	bl_1		1:2:1	12
*Normal vs. physiologic disease II (browning of entire plant).	bl_2		3:1	12
Normal vs. blackleaf	bl_3	lk	3:1	8
Cercospora resistance vs. susceptibility	Ca_1, Ce_4	ce	3:1, 15:1, 63:1, 255:1	7, 10, 11

[1] Authors here reviewed are in general supplemental, in the sense of updating, to those cited by Kadam and Ramiah in their 1943 study, Symbolization of Genes in Rice. However, 4 citations supplement those of Kadam and Ramiah for the period 1938-42. Three of these 4 citations are found in Kadam and Ramiah--with reference to other symbolization (see table 1, citations 5, 8, 17).

[2] Symbols for basic genes are in parentheses. [3] Numbers refer to a list of references following this table.

*Mutation in Caloro variety.

Articles on Inheritance and Symbolization of Genetic Characters in Rice as Reported (Entirely From the United States) Since About 1940

1. Bollich, C. N. (1957). Inheritance of several economic characters in rice. Unpublished thesis, La. State Univ.

2. Breaux, N. (1940). Character inheritance, factor interaction, and linkage relations in the F_2 of a rice cross. Unpublished thesis, La. State Univ., 38 pp.

3. Crane, L. E. (1957). An evaluation of three methods of analyzing the inheritance of quantitative characters in rice. Unpublished thesis, Univ. of Calif.

4. De la Houssaye, DeB. A. (1942). Independent assortment, interaction of factors and linkage studies in the F_2 of a rice cross. Proc. La. Acad. Sci. 6: 52-59.

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7. Jodon, N. E. (1944). The inheritance of flower fragrance and other characters in rice. J. Amer. Soc. Agron. 36: 844-848.

8. Jodon, N. E. (1957). Inheritance of some of the more striking characters in rice. J. Hered. 48: 181-192.

9. Jodon, N. E., and Beachell, H. M. (1943). Rice dwarf mutations and their inheritance. J. Hered. 34: 155-160.

10. Jodon, N. E., and Chilton, S. J. P. (1946). Some characters inherited independently of reaction to physiologic races of Cercospora oryzae in rice. J. Amer. Soc. Agron. 38: 864-872.

11. Jodon, N. E., Ryker, T. C., and Chilton, S. J. P. (1944). Inheritance of reaction to physiologic races of Cercospora oryzae in rice. J. Amer. Soc. Agron. 36: 497-507.

12. Jones, J. W. (1952). Inheritance of natural and induced mutations in Caloro rice, and observations on sterile Caloro types. J. Hered. 43: 81-85.

II. LINKAGE GROUPS IN RICE

Dr. A. H. Sturtevant[7] states: "...there remains much for the geneticist to do in studying the mechanics of segregation and crossingover by his own precise methods. Such studies have not recently been as widely prosecuted as formerly, but I want to insist here that the law of diminishing returns has not set in in this field."

With rice, as with cotton,[8] only recently has comprehensive search for linkage been undertaken.

The possibly paired combinations of recognized characters in rice have been tested in only a few cases. Many of the published genetic studies deal with one character pair at a time and yield no information on linked inheritance. Linkage tests should be made a part of any study of Mendelian characters in rice.

With 12 chromosomes, the chances of finding linkage between any two pairs of characters are rather small. However, for corn, with 10 chromosomes, rather complete linkage maps are available. The corn chromosomes carrying the respective linked groups of genes have, moreover, been identified by appropriate cytological methods.

The best known linkage in rice, between waxy endosperm and apiculus color, was reported by Yamaguchi in 1921 (21).[9] Parnell et al. (17) reported in 1917 the first finding of linkage, one between blackhull and colored internode. Chao (4) in 1928 reported three definite cases of crossingover, including that in the waxy group and the one between purple stigma and purple leaf sheath. Matsuura (13) in 1933 summarized published reports on linkage relations, and Nagao (15) in 1951 published data on the four linkage groups found by workers in Japan up to that time. Published reports up to 1955 were summarized by Jodon (9), at which time it appeared that the accumulated data pertained to perhaps no more than eight groups.

Nagao and Takahashi (16) in 1960 published further linkage data from their studies conducted principally with Japanese varieties. They now indicate 12 groups corresponding to the 12 haploid chromosomes. They have established the linear order of six genes in Group 2 and of three genes in three other groups. Six groups are based on a crossingover between two genes, and two are based on a single gene each for which no linkage with any of the other groups has been found. Diagrams showing these groups are included below, and other published data are placed with the respective groups to which they possibly pertain.

The work of Nagao and Takahashi (16) is a challenge to rice geneticists to further develop the linkage maps by determining the location of additional genes found. Multiple marker stocks should be built up to make possible the assignment of new or untested mutations to their respective linkage groups. Viable, easily identified mutations obtained by irradiation would be valuable for use in linkage studies. Cytogeneticists eventually may be able to identify linkage groups in rice with specific chromosomes.

Linkage studies are suitable research problems for advanced students. Practical plant breeders sometimes make use of correlation studies on the quantitative type of inheritance so often involved in agronomic characters, and in some instances it may be possible to show association of some of the genes involved with known linkage groups. Fortunately, the linkage of favorable and unfavorable genes has apparently been of little hindrance to the progress of rice breeding programs.

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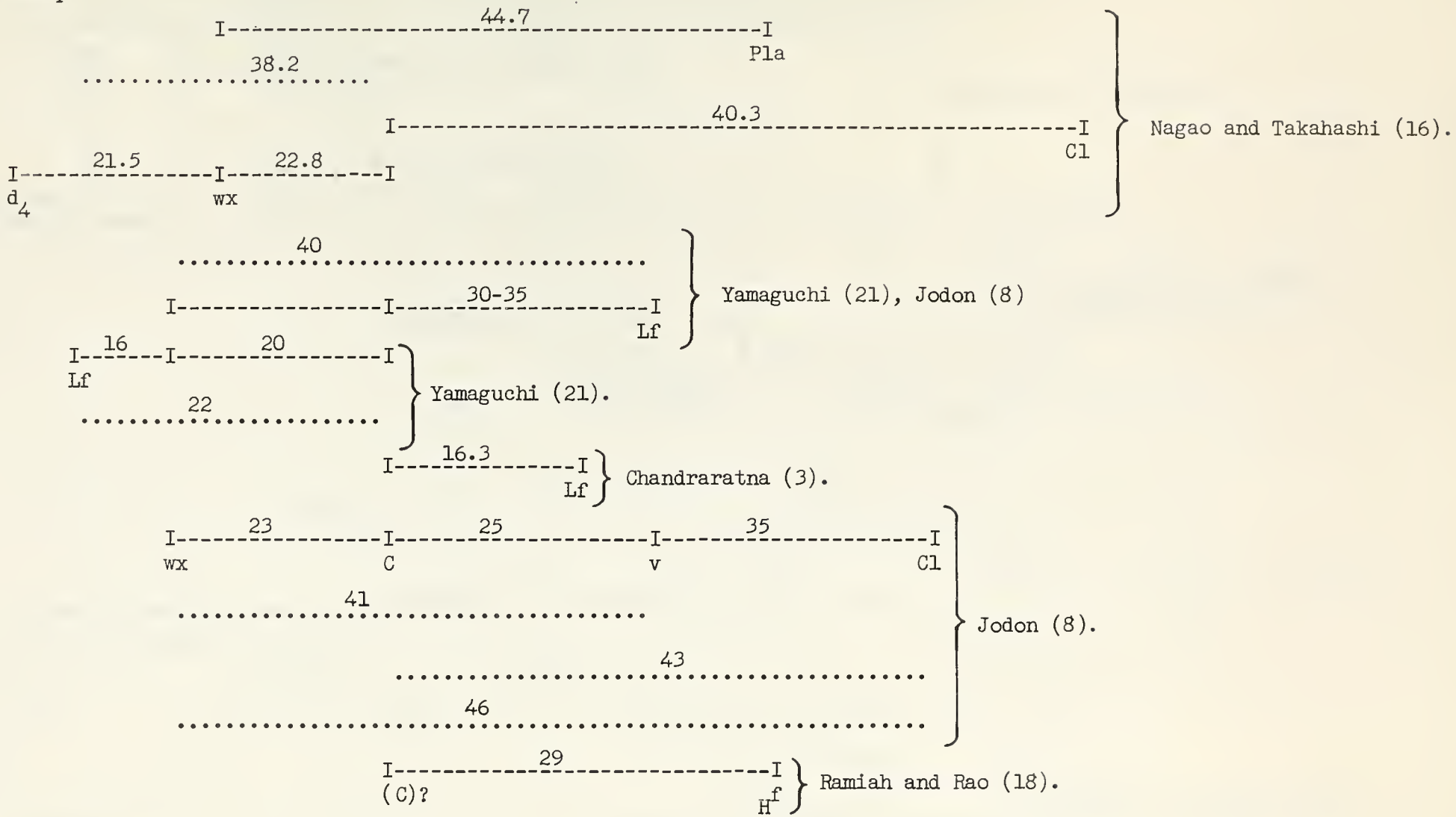
[7] Sturtevant, A. H. (1951). The relation of genes and chromosomes. In Dunn, L. C., ed., Genetics in the 20th century, pp. 101-110 (Ch. 6).

[8] Stephens, S. G. (1955). Linkage in Upland cotton. Genetics 40: 903-917.

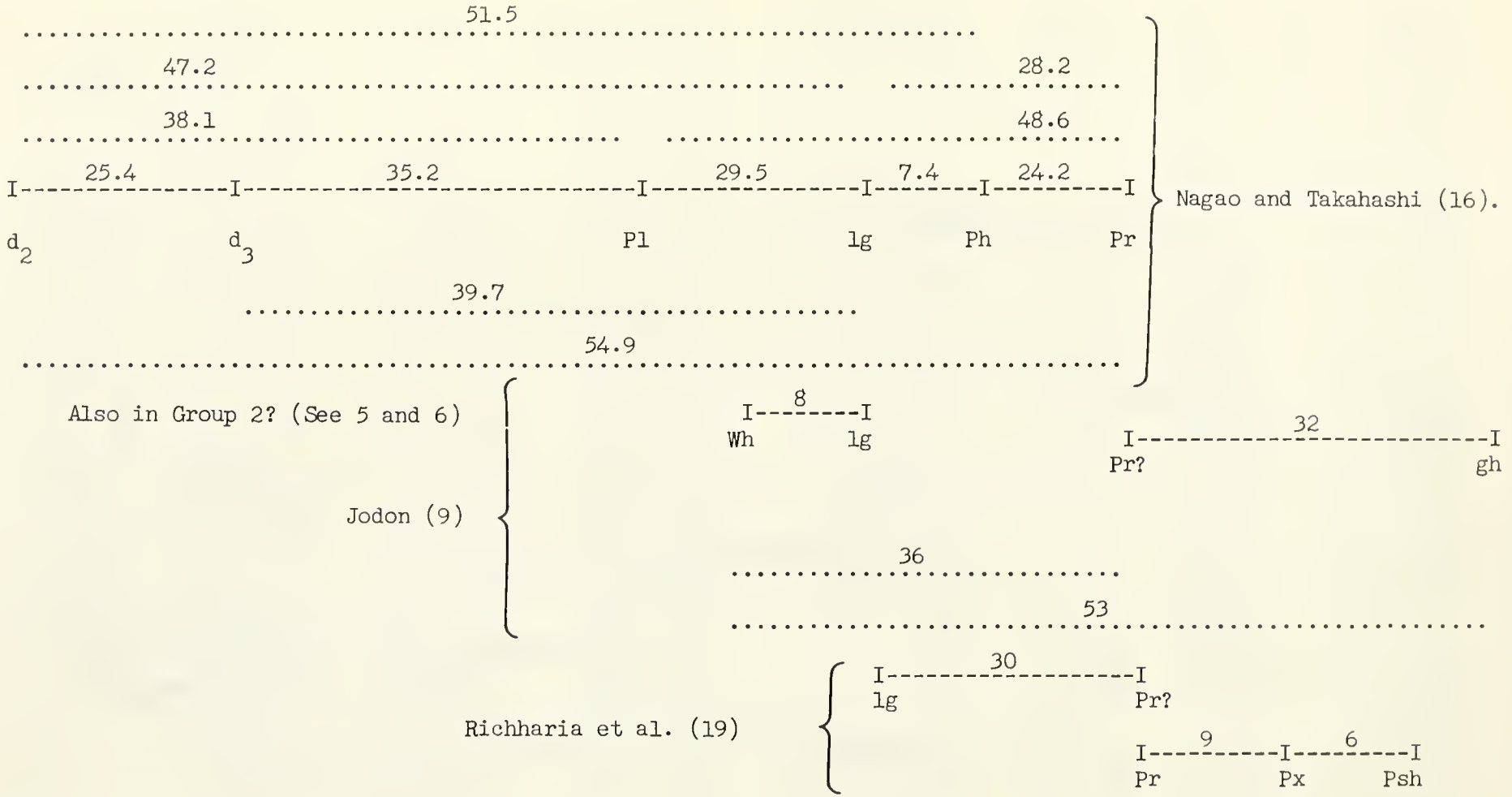
[9] Numbers in parentheses refer to Key Literature and other Reports on Linkage in Rice, p. 56.

Linkage Groups of Nagao and Takahashi (16), 1960
(With other reported linkages inserted in the respective groups to which they may belong)

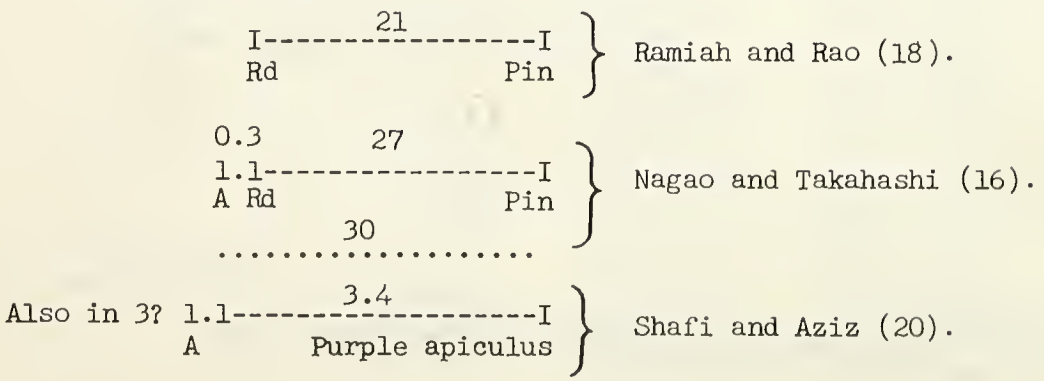
1. "Waxy" Group.



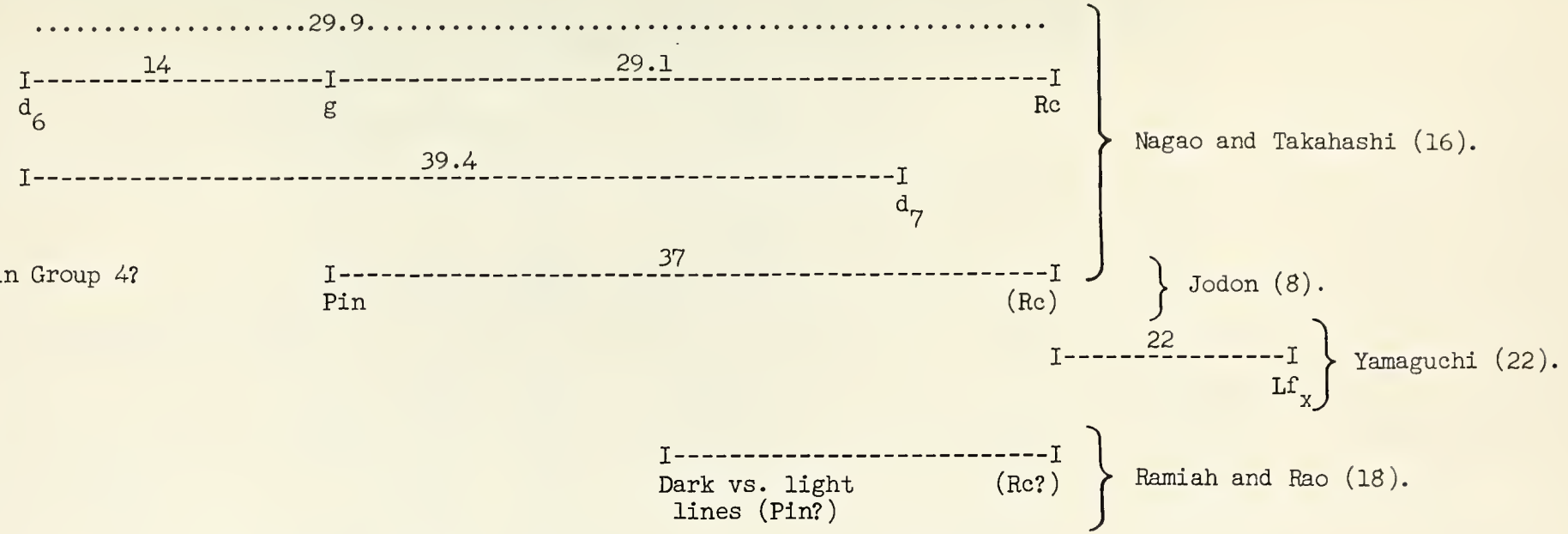
2. "Purpleleaf" Group.

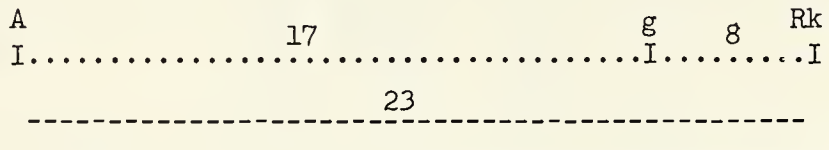


3. "Activator" Group.



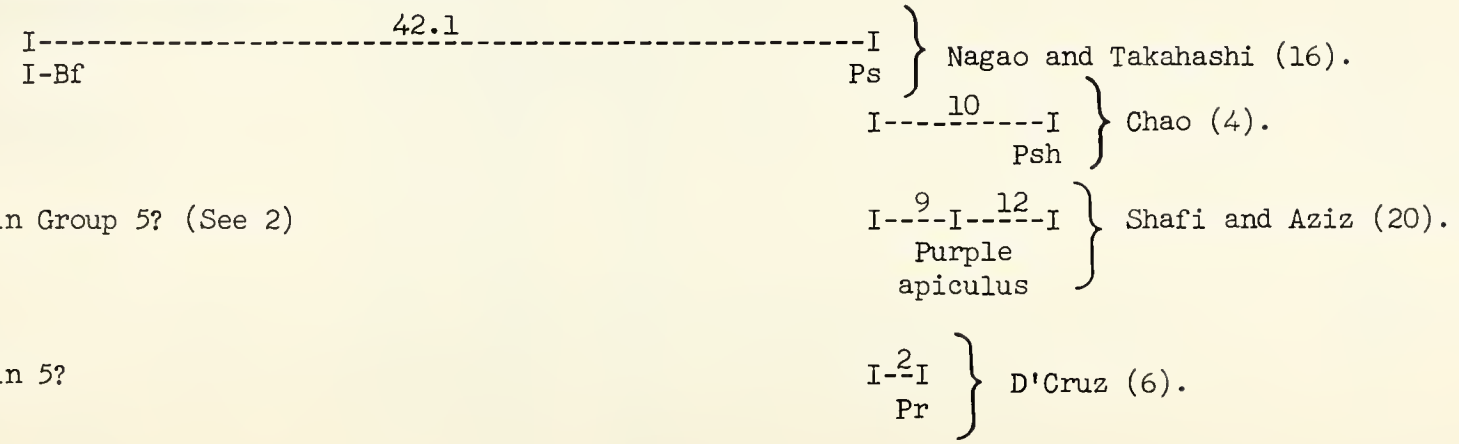
4. "Long Glume" Group.



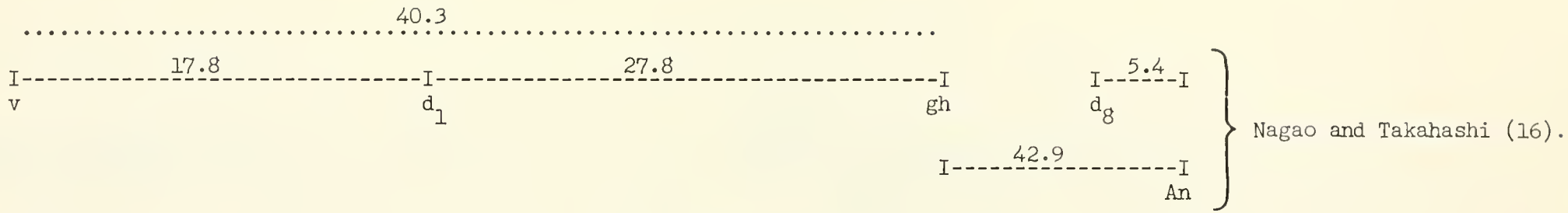


*Duplicate gene segregation for long-glume. (See 3)

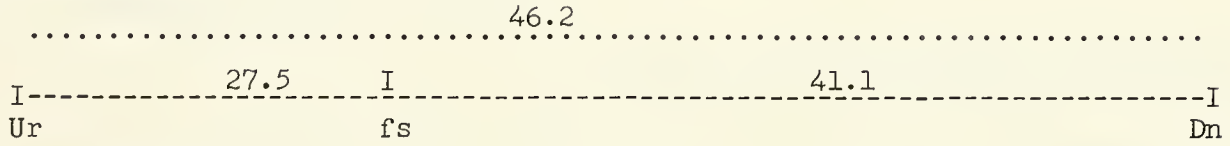
5. "Dark Furrow Inhibitor" Group.



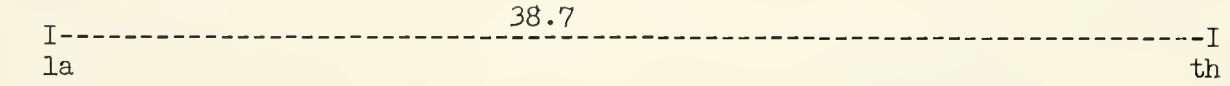
6. "Dwarf" Group.



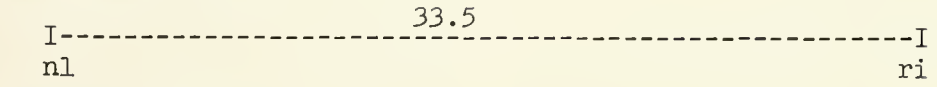
7. "Fine Stripe" Group.



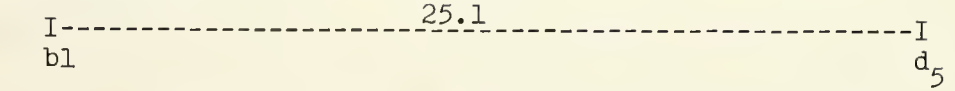
8. "Lazy" Group.



9. "Neckleaf" Group.

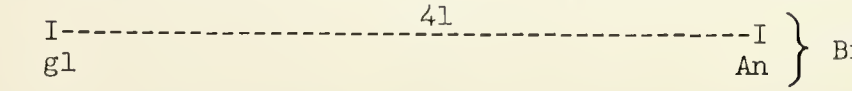


10. "Mottled Blackleaf" Group.



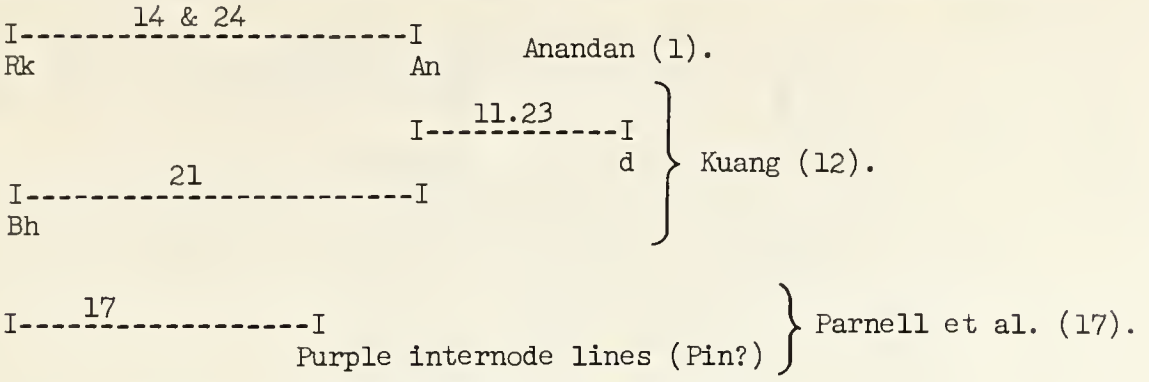
11. "Brittle Culm" Group. (No linkage with bc found by Nagao & Takahashi (16).)

12. "Glabrous" Group. (No linkage with gl found by Nagao & Takahashi (16).)



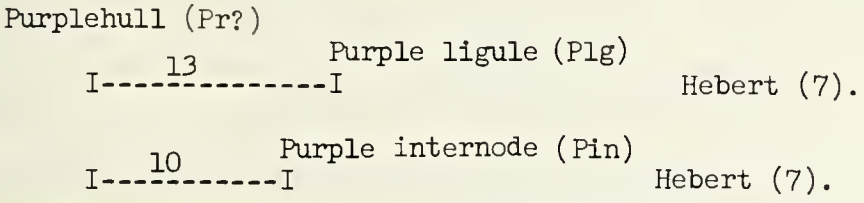
Miscellaneous Linkage Data

A. Linkages with Awn and Blackhull genes. (See Group 12 previous section)

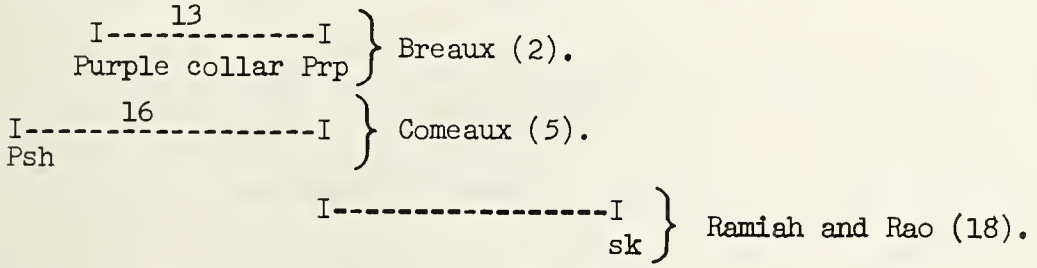


Blackhull vs. Strawhull (ripe stage) gave 27% crossingover with H^i vs. H^f (green stage); Ramiah & Rao (18).

B. Linkages between Purple genes. (See Group 2)



C. Linkages with Purple pericarp (Prp) (bran) genes.



D. Color in the following organs usually is inherited as a unit and independently of wx: Apiculus, lemma, stigma, ligule, auricle, collar, axil, internode, septum, leaf sheath lines; Ramiah & Rao (18).

E. Color in the following organs usually is inherited as a unit and independently of the above and of wx: Completely purple leaf sheath and duplicate genes for purple ligule, auricle, and collar (junctura); Ramiah & Rao (18). (Possibly the Pl gene?)

F. Shattering linked with resistance to Piricularia with about 20% crossingover; Nakamori (1936) as reported by Nagai (14, p. 369).

Key Literature and Other Reports on Linkage in Rice

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4. Chao, L. F. (1928). Linkage studies in rice. Genetics 13: 133-169.
5. Comeaux, D. J. (1946). An inheritance and linkage study of virescence and other factors in rice, Oryza sativa. Unpublished thesis, La. State Univ., 50 pp.
6. D'Cruz, R. (1960). A linkage between two basic genes for anthocyanin colour in rice. Sci. and Cult. [India] 25: 534-536.
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8. Jodon, N. E. (1948). Summary of rice linkage data. U. S. Bur. Plant Indus., Soils, and Agr. Engin., Div. Cereal Crops and Dis. [Mimeo.], 34 pp.
9. Jodon, N. E. (1955-56). Present status of rice genetics. J. Agr. Assoc. China (n.s.) 10: 5-21, 1955; Revision of figures 3 to 6, "Present status of rice genetics." J. Agr. Assoc. China (n.s.) 14: 69-73, 1956.
10. Jodon, N. E., and Chilton, S. J. P. (1946). Some characters inherited independently of reaction to physiologic races of Cercospora oryzae in rice. Agron. J. 38: 864-872.
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13. Matsuura, H. [A.] (1933). Oryza sativa. In his A bibliographical monograph on plant genetics (genic analysis), 1900-1929. Ed. 2, pp. 240-265. Hokkaido Imp. Univ., Sapporo.
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16. Nagao, S., and Takahashi, M. (1960). Genetical studies on rice plant, XXIV. Preliminary report of twelve linkage groups in Japanese rice. J. Faculty Agr., Hokkaido Univ. [Sapporo] 51: 289-298
17. Parnell, F. R., Rangaswami Ayyangar, G. N., and Ramiah, K. (1917). The inheritance of characters in rice, I. Mem. Dept. Agr. India, Bot. Ser., 9: 75-105.
18. Ramiah, K., and Rao, M. B. V. N. (1953). Rice breeding and genetics. Sci. Monog. Indian Council Agr. Res. 19, 360 pp.
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20. Shafi, M., and Aziz, M. A. (1959). The inheritance of anthocyanin pigment in the outerglume and apiculus of rice. Agr. Pakistan 10: 217-232.
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